



# Long-term realised and projected growth impacts caused by autumn gum moth defoliation of 2-year-old *Eucalyptus nitens* plantation trees in Tasmania, Australia

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## ABSTRACT

Insect damage to production forests has the potential to reduce financial returns by retarding tree growth and causing mortality, however, long-term realised quantification of these losses is rare. In order to help elucidate economic damage thresholds for making spray decisions we capitalised on a natural outbreak of autumn gum moth, *Mnesampela privata*, in a 2-year-old *Eucalyptus nitens* plantation. Following the partial chemical control of this insect outbreak we measured the tree growth variables diameter at breast height over bark and height of five differing tree defoliation classes for 75 months following tree damage. At the end of this period a threshold model was fitted to describe the relationship between tree defoliation and realised tree wood volumes. The model revealed that realised stand wood volume was not significantly affected up until defoliation exceeded 60% and then declined sharply after this defoliation level was reached. Further support for this defoliation threshold was evident from multiple comparisons among defoliation classes that showed 50% defoliated trees did not have significantly different wood volume compared to more lightly defoliated trees, but did have significantly greater wood volume compared to trees that were 72% or more defoliated. To determine if the realised differences in wood volume resulted in differences in yield over a plantation rotation the *E. nitens* growth model NITGRO was used to on-grow trees to age 15 years for a 'best case' (type 1 growth response, constant growth rates from last inventory until harvest) and 'worst case' (type 2 growth response, divergent growth rates from last inventory until harvest) scenario. The threshold model was then fitted to the outcomes of both scenarios and the economic consequences of defoliation were clearly dependent on the growth function assumed.

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## 1. Introduction

Hardwood plantations in Australia continue to expand each year as the forest industry increases its reliance on plantation forestry for wood products and moves toward an overall forest plantation estate of three million hectares by 2020 (AFFA, 1997). By the year 2008 a total of 950,000 ha of hardwood plantations had been established across Australia with 61% of these plantations being *Eucalyptus globulus* Labill. and 19% *E. nitens* (Deane and Maiden) Maiden (BRS, 2009). *Eucalyptus* plantations represent a monoculture of uniform species, age, spacing and often genetic composition, providing ideal conditions for insect

outbreaks (Bassman and Dickmann, 1985). The implications of foliage loss from insect feeding on eucalypt growth range from negligible growth reductions after partial defoliation (Landsberg and Ohmart, 1989; Matsuki et al., 2007) to retardation of tree growth and tree mortality after severe defoliation (Cremer, 1966; Greaves, 1966; Candy et al., 1992; Jordan et al., 2002). It should be noted however that growth responses are not just determined by the severity of damage, as frequency of occurrence, location of damage within the canopy, the age damage occurs, timing of damage, tree vigour and species of host tree may all influence growth responses (Cremer, 1966; Stone, 2001; Collett and Neumann, 2002; Floyd and Farrell, 2007).

Artificial defoliation has been frequently used to assess the impacts of foliage loss on tree growth (e.g. Pinkard et al., 2006a). However, such studies may not necessarily reveal how a specific insect pest will alter tree growth rates as it can fail to replicate the damage caused to a plant by a defoliating insect, especially given differing feeding behaviours that occur among different

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insect species. This study investigates the growth responses of 2-year-old *E. nitens* plantation trees following defoliation caused by *Mnesampela privata* Guenée (Lepidoptera: Geometridae), a serious and frequently occurring pest of eucalypt plantations throughout southern Australia (McQuillan, 1985; Abbott, 1993; de Little et al., 2008).

Despite the potential of insect damage to reduce financial returns from plantations through reducing wood volume obtained at harvest, few studies have analysed stand growth following various intensities of defoliation and extended predictions to the end of rotation (but see Candy, 2000). This is because monitoring tree growth from the time of damage to the point of harvest is rarely practical. Therefore, decisions such as if to spray insecticide to control an insect outbreak must be made in the interim based on the best available information at hand. To this end predictive modelling of tree growth can yield significant insights. Snowdon (2002) identified two types of tree growth responses to fertiliser application, which are equally applicable to tree growth after defoliation. The first is a type 1 growth response where an initial decrease in growth is observed after tree damage, but is not sustained in the long-term and hence leads to parallel growth trends with undamaged trees (Snowdon, 2002). The second is a type 2 growth response in which growth trends are indefinitely reduced resulting in a sustained change in tree productivity causing divergent growth trends from undamaged trees (Snowdon, 2002). A type 1 growth response is the 'best case' scenario whereas a type 2 is the 'worst case' scenario. In the present study we used both scenarios to calculate the upper and lower boundaries for wood yields achieved at harvest.

In the year 2000 the partial control, by aerial spraying, of an outbreak of *M. privata* in a *E. nitens* plantation led to a unique situation where large differences (5–100% defoliation) in tree defoliation levels occurred in close proximity to each other, which was ideally suited to comparing growth rates of trees defoliated to varying levels by this pest. Defoliation caused by *M. privata* larvae can result in poor tree form, reduced growth rates (Abbott, 1993) and in severe cases tree mortality (Elliott and Bashford, 1978; Farrow et al., 1994). In this study we monitored tree growth for 75 months following a single summer defoliation event that occurred prior to canopy closure. Furthermore, we undertook predictive modelling to estimate the impact of this defoliation event on wood yield for a 15-year plantation rotation. We chose a 15-year period as this is a typical age at which eucalypt plantations are harvested for pulp (Jenkin, 1990; Mercer and Underwood, 2002) and used both a type 1 and type 2 growth response (Snowdon, 2002) in the *E. nitens* growth model NITGRO (Candy, 1997).

## 2. Materials and methods

### 2.1. The pest insect

The host range of *M. privata* encompasses many *Eucalyptus* species (Elliott and Bashford, 1978; Neumann and Collett, 1997; Lukacs, 1999), including Australia's major pulpwood plantation species *E. nitens* and *E. globulus*. *M. privata* is a sporadic 'gradient' outbreak species (Steinbauer, 2002) that if left unchecked is capable of completely stripping whole trees of foliage (Lukacs, 1999). While *M. privata* generally displays a univoltine lifecycle, in which female adults oviposit in the autumn, under appropriate environmental conditions it may display a bivoltine lifecycle in which female moths oviposit in both autumn and summer (Lukacs, 1999). The outbreak of *M. privata* that caused the tree defoliation monitored in the present study was the result of a 'second-generation' summer outbreak. Both *E. nitens* and *E. globulus* are strongly heteroblastic switching from juvenile to adult foliage between two and four years of age (Jordan et al., 2000), however,

*M. privata* principally oviposit on juvenile foliage in the field and therefore larvae are only a pest of young trees. Nevertheless, in plantations where trees display both juvenile and adult foliage initial larval development can occur on juvenile foliage in the lower tree canopy and when this foliage type is exhausted larvae may consume adult foliage to complete their development (Floyd, 1997). During development, larvae undertake two distinct feeding patterns; the young larvae skeletonise the leaf surface avoiding essential oil glands, while older larvae (third instar onwards) are able to consume foliage at a vastly increased rate as they are able to utilise the whole leaf.

### 2.2. Plantation site and insect outbreak

The defoliated trees used in this study were identified in a two-year-old *E. nitens* plantation at Mawbanna (40°57'S, 145°21'E) in north-western Tasmania. The plantation was established in December 1998 on a ferrosol soil, which had previously been used as a dairy pasture. Trees were planted at a rate of 1150 stems per hectare. The site received 1500 mm of rainfall per annum and no fertiliser was applied to the plantation throughout the study period. In December 2000, trees were all in juvenile foliage phase and a severe outbreak of *M. privata* was observed in the plantation with an oviposition survey of forty trees revealing an average of  $55 \pm 4$  egg batches (range 7–129) per tree when each tree was searched for 3 min. To limit tree damage caused by larval feeding an aerial application of a synthetic pyrethroid contact insecticide was undertaken in January 2001. However, due to the insecticide's solubility and toxicity to aquatic life, plantation trees bordering a nearby watercourse could not be sprayed (K. Smith, Forest Enterprises, personal communication). As a consequence of the spraying, at the cessation of larval feeding (March 2001) trees in close spatial proximity to each other displayed a wide variety of defoliation levels. These ranged from severe defoliation (100%) to minimal defoliation (<5%) with the levels of defoliation varying throughout the whole plantation. The plantation was thus chosen to study the effects of defoliation on subsequent tree growth and no other major pathogen or insect defoliation event occurred over the period of the trial.

### 2.3. Experimental replicates

Twenty-two experimental replicates were established in the area of the plantation where tree defoliation variability was observed. Each replicate contained one tree in each of the following defoliation classes; 1–20% (average across all trees in class: 10%), 21–40% (average: 28%), 41–60% (average: 50%) and 61–80% (average: 72%), as well as two trees in a severely defoliated class, 81–100% (average: 90%) to compensate for an expected increased mortality in this class. Defoliation classes are henceforth referred to as their averages. Trees were designated a defoliation class after the percentage of total crown loss had been independently estimated by two scorers to the nearest 5%. Trees within each replicate were kept in close proximity to each other (within a 30 m radius) in an attempt to minimise any effect of environmental variation and replicates did not overlap. Some replicates comprised of the five defoliation classes were located on the edge of the plantation, however the majority were sourced within the plantation. In July 2001, four months after cessation of any tree damage, the breast height (1.3 m) over bark diameter (diameter) and height of all experimental trees were first recorded. Subsequent diameter and height measurements were undertaken in January 2002, August 2002, March 2003, May 2004, February 2005 and June 2007 (10, 17, 24, 38, 47 and 75 months after trees were damaged). Over the duration of the experiment five (11%) of the trees belonging to the 90% defoliation class died early, no other

tree deaths were recorded in the more lightly defoliated classes. Furthermore, throughout the course of the experiment a number of trees lost identifying markers hence the total number of trees assessed reduced with time from 132 to 111 for which growth measurements were available. Trees which died early in the experiment were not included in overall calculations of wood volume recorded for a 15-year harvest.

#### 2.4. Data analyses

Following Hodge et al. (1996) tree volume ( $\text{m}^3$ ) was estimated using diameter at breast height (1.3 m) over bark ( $d$ ) and total tree height ( $h$ ) using the formula:

$$\text{Volume} = 1.3 \left( \frac{d}{2} \right)^2 + \left( \frac{1}{3} \right) \left( \frac{d}{2} \right)^2 (h - 1.3) \quad (1)$$

Differences in tree height, diameter and volume between defoliation classes were analysed with log transformed data using the General Linear Model Repeated Measures procedure of SPSS (Version 16.0, SPSS Inc.). Time and the time by defoliation class interaction were fitted within subjects (trees) and the defoliation class (fixed), replicate (random) and their interaction (random) effects were fitted as the between subject effects. Subsequent analyses were undertaken at each time on log transformed data separately fitting defoliation class, replicate and interaction effects using the General Linear Model, Univariate procedure of SPSS (Version 16.0, SPSS Inc.). Significance tests were undertaken using a Type III Sum of Squares and the random replicate by defoliation class interaction used to test the significance of the fixed defoliation class effect. Also investigated was whether tree defoliation had a greater effect on tree diameter or tree height. This was achieved by determining, for each defoliation class, whether the proportion of reduction in tree diameter compared to trees in the 10% defoliation class was different to the proportion of reduction in tree height compared to trees in the 10% defoliation class.

#### 2.5. Growth modelling and economic evaluation

The observed diameter at breast height and height measurements for each tree at 75 months after defoliation were extrapolated to stand wood volume and economic value per hectare using the *E. nitens* empirical stand growth model NITGRO (Candy, 1997; Pinkard and Battaglia, 2001). The model uses a suite of empirical growth and yield functions developed for *Eucalyptus nitens* plantations in Tasmania and New Zealand (Candy, 1997). The model requires as an input the site index, SI (m), defined to be the mean dominant height at age 15 years, and stand basal area. These were calculated from the inventory data.

A plantation stocking rate of 950 trees per hectare was assumed. Using this growth model trees were then on-grown from the last inventory (75 months post defoliation) to 15 years (harvest age) to predict the long-term consequences of age 2 years defoliation. Two approaches were used in this modelling. The first was a 'best case' approach. In this case a type 1 growth response was assumed. That is, the only effect of defoliation was assumed to be the volume loss recorded at the time of the last inventory. All trees irrespective of defoliation level were subsequently on-grown using a site index derived from the stand volume at age 8.5 years (the last measurement) by inverting the volume equation based on the average of predicted stand volume of all eight trees with the least defoliation level scored of 5%. It is assumed that defoliation effects at this level were negligible. The second approach, used as a 'worst case', was to assume the site index was variable for each tree and was estimated from its stand volume

projections at age 8.5 years, the time of the last inventory. This implies a type 2 growth response or residual long-term impact of defoliation. In reality the actual response was expected to be somewhat intermediate and the 'best case' and the 'worst case' can be seen bounding the likely impact.

A threshold model (MacArthur, 1957) was used to describe the relationship between percentage tree defoliation at age 2 years and its realised stand wood volume per hectare of individual trees 75 months after tree damage, as well as predicted stand wood volume per hectare of individual trees at age 15 years for both a type 1 and type 2 growth response. The threshold model was fitted using the Solver option in Excel to minimise the sum of squares deviation between observed and predicted values. The parameters estimated by Solver included mean tree growth in the absence of defoliation, a defoliation threshold for reductions in tree growth, as well as the slope and y-intercept for any determined negative relationships between defoliation and tree growth. Using the plantation floor price of AUD\$27.00 per green cubic metre (Forestry Tasmania, 2007) gross revenue was also included in these calculations.

### 3. Results

There was a significant effect of time (height  $F = 2643$ , diameter  $F = 1417$ , volume  $F = 1859$ ; all  $F_{6,504}$ ;  $P < 0.001$ ), tree defoliation class (height  $F = 15.4$ , diameter  $F = 27.8$ , volume  $F = 29.4$ ; all  $F_{4,84}$ ;  $P < 0.001$ ) and the interaction of time and defoliation class (height  $F = 11.5$ , diameter  $F = 12.1$ , volume  $F = 13.3$ ; all  $F_{24,504}$ ;  $P < 0.001$ ) on all three growth variables over the 75 months trees were monitored after damage. At the final inventory (75 months following tree damage) the threshold model accounted for 24% of the variation in stand wood volume and revealed that a mean stand wood volume of  $169 \text{ m}^3/\text{ha}$  was maintained up until 61% defoliation (Fig. 1). Above this level of defoliation a negative linear regression (slope:  $-3.3$ , y-intercept:  $372 \text{ m}^3/\text{ha}$ ) was observed between tree defoliation at age 2 years and realised wood volume (Fig. 1).

At the first inventory, four months after tree defoliation and at the time tree damage was assessed, each class had a similar volume (Table 1) and diameter (Table 2). The only difference recorded was for tree height with the more heavily defoliated trees (72 and 90% defoliation classes) being significantly taller compared to trees that were 10% defoliated (Table 3). The first significant negative effects of tree defoliation on tree growth were recorded at the second inventory, 10 months after damage. At this time the 10 and 28% defoliated tree classes had significantly more volume compared to more heavily defoliated classes (Table 1), and also had significantly greater volume gains between 4 and 10 months after tree damage

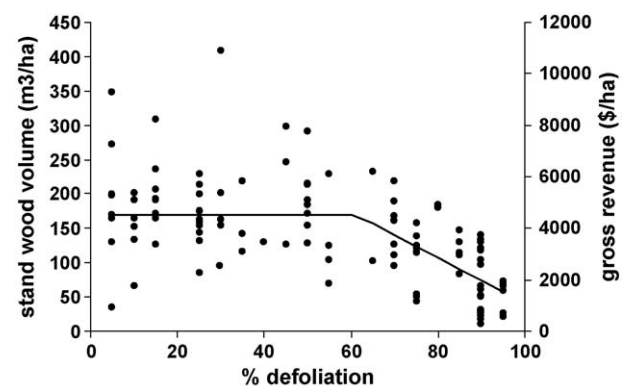
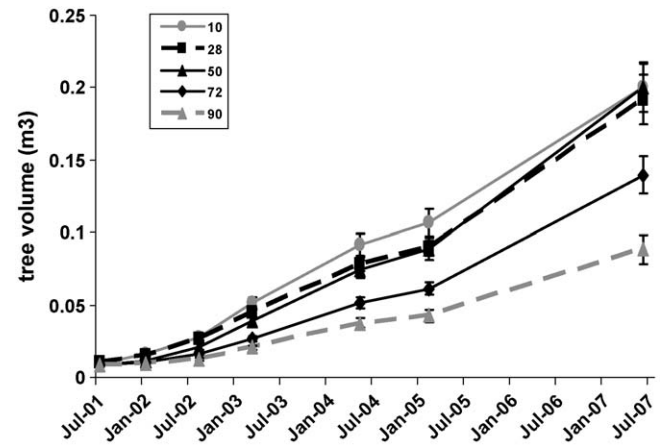


Fig. 1. Threshold model fitted between percentage tree defoliation of individual *E. nitens* trees and realised stand wood volume per hectare 75 months after tree damage. Gross revenue of stand wood volumes per hectare has been included on a second y-axis.

**Table 1**  
Comparisons between different defoliation classes (mean defoliation: 10, 28, 50, 72 and 90%) of *E. nitens* plantation trees for mean  $\pm$  SE tree volume 4, 10, 17, 24, 38, 47 and 75 months after tree defoliation and for mean  $\pm$  SE volume gains from the previous inventory.

Time (months)	4	10	17	24	38	47	75
10%	0.009a (0.001)	0.016a (0.002)	0.028a (0.002)	0.051a (0.002)	0.092a (0.008)	0.107a (0.009)	0.200a (0.017)
28%	0.010a (0.002)	0.016a (0.001)	0.026a (0.002)	0.045a (0.003)	0.078a (0.005)	0.089a (0.005)	0.192a (0.017)
50%	0.009a (0.001)	0.012b (0.001)	0.021ab (0.002)	0.039a (0.003)	0.075ab (0.006)	0.089a (0.007)	0.200a (0.017)
72%	0.009a (0.001)	0.011b (0.001)	0.016bc (0.001)	0.027b (0.002)	0.052b (0.004)	0.061b (0.004)	0.140b (0.013)
90%	0.009a (0.001)	0.010b (0.001)	0.013c (0.001)	0.021c (0.002)	0.037c (0.003)	0.043c (0.004)	0.088c (0.010)
$F_{4,84 \text{ to } 71}$	0.9	17.1	52.0	43.0	36.5	34.1	18.3
Prob.	0.469	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Tree volume gains ( $\text{m}^3 \pm$ SE)							
10	0.007a (0.001)	0.012a (0.001)	0.012a (0.001)	0.023a (0.003)	0.040a (0.005)	0.051a (0.002)	0.094a (0.010)
28	0.006b (0.001)	0.010b (0.001)	0.010b (0.001)	0.019b (0.002)	0.033ab (0.003)	0.041ab (0.002)	0.102a (0.015)
50	0.003c (0.000)	0.010b (0.001)	0.010b (0.001)	0.018b (0.001)	0.036a (0.003)	0.044a (0.002)	0.111a (0.012)
72	0.002d (0.000)	0.005c (0.000)	0.005c (0.000)	0.011c (0.001)	0.025bc (0.002)	0.030ab (0.001)	0.078ab (0.009)
90	0.001e (0.000)	0.003d (0.000)	0.003d (0.000)	0.008c (0.001)	0.017c (0.002)	0.025b (0.001)	0.046b (0.006)
$F_{4,84 \text{ to } 71}$	193.5	115.5	61.4	20.7	5.6	13.6	<0.001
Prob.	<0.001	<0.001	<0.001	<0.001	0.008	<0.001	<0.001

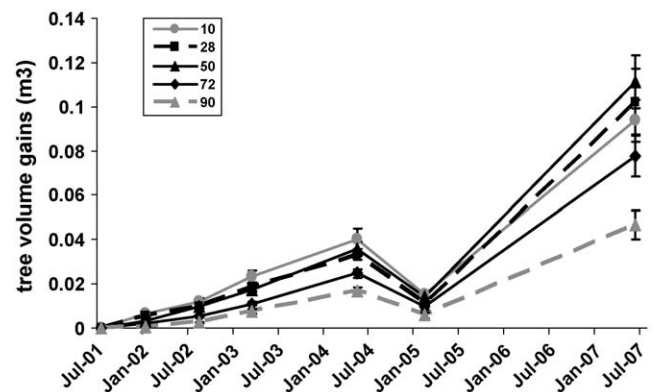
At the first inventory  $n = 22$  trees per defoliation class, apart for trees in the 90% defoliation class where  $n = 44$ .  $F$ -value, degrees of freedom and probability are reported for the ANOVA conducted at each inventory on  $\log(x+1)$  transformed data. The number of degrees of freedom reduced from 84 to 71 over the course of the experiment due to tree mortality and lost tree identification markers. Superscript letters (a–e) represents post hoc Tukey HSD grouping. Defoliation classes with the same letter did not differ significantly.



**Fig. 2.** Mean tree volume ( $\text{m}^3 \pm$  SE) of different defoliation classes (mean defoliation: 10, 28, 50, 72 and 90%) of *E. nitens* plantation trees 4, 10, 17, 24, 38, 47 and 75 months after tree defoliation. At the first inventory  $n = 22$  trees per defoliation class, apart for trees in the 90% defoliation class where  $n = 44$ .

(Table 1). Tree measurements taken 38, 47 and 75 months after tree damage, revealed that trees that were 50% defoliated did not have significantly different growth rates compared to more lightly defoliated classes (Tables 1–3) and hence their final volume 75 months after tree damage was not significantly less than trees that were more lightly defoliated (Table 1). Therefore, following the initial deleterious response to defoliation in the first year, growth rates of trees defoliated up to and including 50% did not diverge, which is consistent with a type 1 growth response (Figs. 2 and 3).

By 75 months after tree damage, trees that were 72% defoliated had significantly more wood volume than the 90% defoliated trees (Table 1). However, this class also had significantly less wood volume than the more lightly defoliated classes, even though at the 75 month inventory they had similar growth rates to the more lightly defoliated trees (Tables 1–3). Over the duration of the experiment, trees that were 90% defoliated always had suppressed growth rates compared to more lightly defoliated classes (Tables 1–3). Further, volume gains of the 90% defoliation class were always significantly less than trees in the 10% defoliation class (Table 1), consistent with a type 2 growth response. Growth achieved by the 90% defoliated class is even further reduced if the 11% tree mortality is included in wood volume calculations. For example, 75 months after tree damage, mean tree volume for the 90% defoliated class when tree mortality was not included was  $0.088 \text{ m}^3$ , but when calculated including tree mortality mean tree



**Fig. 3.** Mean tree volume gains ( $\text{m}^3 \pm$  SE) from the previous inventory of different defoliation classes (mean defoliation: 10, 28, 50, 72 and 90%) of *E. nitens* plantation trees 4, 10, 17, 24, 38, 47 and 75 months after tree defoliation. At the first inventory  $n = 22$  trees per defoliation class, apart for trees in the 90% defoliation class where  $n = 44$ .



**Table 2**

Comparisons between different defoliation classes (mean defoliation: 10, 28, 50, 72 and 90%) of *E. nitens* plantation trees for mean  $\pm$  SE diameter 4, 10, 17, 24, 38, 47 and 75 months after tree defoliation and for mean  $\pm$  SE diameter gains from the previous inventory.

Time (months)	Diameter (mm)± (SE)							Diameter gains (mm)± (SE)					
	4	10	17	24	38	47	75	10	17	24	38	47	75
10%	66.6a (3.9)	84.1a (3.8)	105.3a (4.0)	131.4a (4.8)	164.2a (6.1)	172.8a (6.4)	199.0a (8.3)	17.5a (1.4)	21.2a (1.5)	26.1a (2.0)	32.8ab (3.1)	8.6a (0.8)	26.2a (3.6)
28%	69.6a (3.3)	84.8a (2.9)	103.2a (2.8)	124.7a (3.1)	154.9a (3.5)	162.3a (3.9)	195.5a (6.4)	15.2ab (1.4)	16.9ab (1.3)	21.6ab (1.7)	30.2ab (2.1)	7.4ab (0.7)	33.2a (5.1)
50%	63.9a (3.3)	72.8b (3.3)	93.1ab (3.7)	116.5a (4.0)	150.4ab (4.7)	160.3ab (5.2)	198.4a (7.5)	10.7bc (1.5)	20.1a (1.3)	23.4ab (1.0)	34.0a (2.1)	9.9a (1.0)	38.1a (4.1)
72%	64.7a (2.9)	70.2b (2.9)	83.4bc (2.8)	102.3b (3.0)	131.2b (3.9)	138.0b (4.4)	169.6ab (7.6)	6.0c (0.9)	13.2b (1.2)	18.9b (1.4)	28.9ab (1.6)	6.8ab (1.1)	31.3a (3.8)
90%	64.3a (2.1)	68.1b (1.9)	74.3c (2.2)	89.5c (3.0)	111.3c (4.4)	115.4c (4.9)	135.6c (6.9)	2.1d (0.5)	6.4c (0.9)	13.9c (1.5)	21.8b (1.8)	4.3b (1.2)	20.5a (3.1)
$F_{4, 84 \text{ to } 71}$	1.1	20.1	47.9	38.6	33.5	31.9	17.9	44.0	25.7	17.7	5.8	4.8	1.6
Prob.	0.362	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.006	0.013	0.234

At the first inventory  $n = 22$  trees per defoliation class, apart for trees in the 90% defoliation class where  $n = 44$ .  $F$ -value, degrees of freedom and probability are reported for the ANOVA conducted at each inventory on  $\log(x+1)$  transformed data. The number of degrees of freedom reduced from 84 to 71 over the course of the experiment due to tree mortality and lost tree identification markers.

Superscript letters (a–d) represents post hoc Tukey HSD grouping. Defoliation classes with the same letter did not differ significantly.

**Table 3**

Comparisons between different defoliation classes (mean defoliation: 10, 28, 50, 72 and 90%) of *E. nitens* plantation trees for mean  $\pm$  SE height 4, 10, 17, 24, 38, 47 and 75 months after tree defoliation and for mean  $\pm$  SE height gains from the previous inventory.

Time (months)	Height (m) ± (SE)							Height gains (m) ± (SE)						
	4	10	17	24	38	47	75	10	17	24	38	47	75	
10%	4.54a (0.21)	5.26a (0.22)	6.53a (0.24)	8.15a (0.31)	9.74a (0.34)	10.40a (0.33)	15.86a (0.51)	0.73a (0.08)	1.27a (0.11)	1.61a (0.13)	1.60a (0.14)	0.66a (0.09)	5.46ab (0.42)	
28%	4.80abc (0.20)	5.33a (0.20)	6.54a (0.21)	8.09a (0.27)	9.60a (0.27)	10.13ab (0.26)	15.84a (0.41)	0.53b (0.06)	1.14a (0.13)	1.55a (0.15)	1.51a (0.10)	0.53a (0.08)	5.72ab (0.38)	
50%	4.72ab (0.19)	5.17a (0.21)	6.26a (0.25)	7.92a (0.31)	9.54ab (0.35)	10.17ab (0.33)	16.12a (0.38)	0.47b (0.06)	1.07a (0.12)	1.66a (0.13)	1.62a (0.10)	0.63a (0.08)	5.95a (0.40)	
72%	4.91bc (0.20)	5.10a (0.21)	5.73b (0.23)	6.95b (0.23)	8.53bc (0.28)	9.31bc (0.31)	15.04ab (0.35)	0.25c (0.06)	0.63b (0.09)	1.22b (0.12)	1.58a (0.13)	0.78a (0.10)	5.64ab (0.36)	
90%	5.04c (0.12)	5.21a (0.12)	5.60b (0.24)	6.67b (0.22)	8.01c (0.27)	8.63c (0.27)	13.28b (0.49)	0.08d (0.03)	0.38 (0.07)c	0.99b (0.12)	1.31a (0.12)	0.68a (0.11)	4.72b (0.32)	
$F_{4, 84 \text{ to } 71}$	5.6	0.8	17.3	21.0	20.1	16.7	11.7	62.4	32.6	7.8	2.3	0.6	6.7	
Prob.	0.001	0.528	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.001	0.111	0.690	0.004	

At the first inventory  $n = 22$  trees per defoliation class, apart for trees in the 90% defoliation class where  $n = 44$ .  $F$ -value, degrees of freedom and probability are reported for the ANOVA conducted at each inventory on  $\log(x+1)$  transformed data. The number of degrees of freedom reduced from 84 to 71 over the course of the experiment due to tree mortality and lost tree identification markers.

Superscript letters (a–c) represents post hoc Tukey HSD grouping. Defoliation classes with the same letter did not differ significantly.

volume is reduced to 0.076 m<sup>3</sup>. Interestingly between 38 and 47 months reduced volume gains for all defoliation classes were recorded (Fig. 3), probably as a result of poor seasonal growth during this period.

When measured against the 10% defoliated tree class the loss of diameter was proportionally greater than the loss of height for all defoliation classes (Table 4). For example, 75 months after trees were damaged, the height of trees that were 90% defoliated was

0.84 of that measured for 10% defoliated trees compared to 0.68 for diameter (Table 4).

When individual trees were on-grown to age 15 years under a type 1 growth response the threshold model revealed a mean stand wood volume of 378 m<sup>3</sup>/ha was maintained up until 80% tree defoliation before a reduction in stand tree volume (slope:  $-9.0$ ,  $y$ -intercept: 1097 m<sup>3</sup>/ha) was recorded (Fig. 4). A similar mean stand wood volume of 386 m<sup>3</sup>/ha was achieved under a type 2 growth

**Table 4**

Height ( $h$ ) and diameter ( $d$ ) proportions for each defoliation class (28, 50, 72 and 90%) compared to the 10% class for measurements taken 4, 10, 17, 24, 38, 47 and 75 months after tree damage.

Time (months)	4		10		17		24		38		47		75	
	$h$	$d$	$h$	$d$	$h$	$d$	$h$	$d$	$h$	$d$	$h$	$d$	$h$	$d$
28%	1.06	1.05	1.01	1.01	1.00	0.98	0.99	0.95	0.98	0.94	0.97	0.94	1.00	0.98
50%	1.04	0.96	0.98	0.87	0.96	0.88	0.97	0.89	0.98	0.92	0.98	0.93	1.02	1.00
72%	1.08	0.97	0.97	0.84	0.88	0.79	0.85	0.78	0.88	0.80	0.90	0.80	0.95	0.85
90%	1.11	0.97	0.99	0.81	0.86	0.71	0.82	0.68	0.82	0.68	0.83	0.66	0.84	0.68

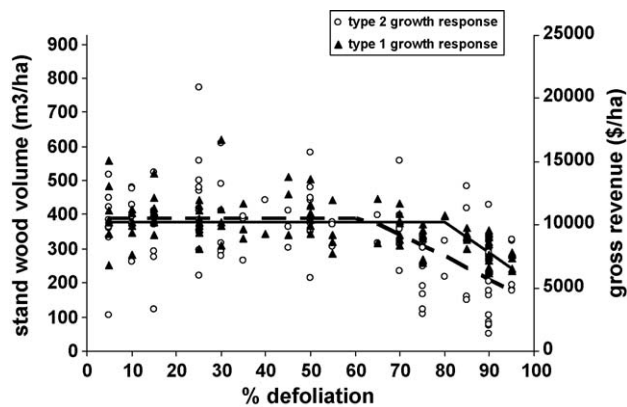


Fig. 4. Threshold model fitted between percentage tree defoliation and predicted stand wood volume per hectare of individual *E. nitens* trees at age 15 years for a type 1 growth response (the best case—black triangles with a black line) and a type 2 growth response (the worst case—white circles with a dashed line). Gross revenue of stand wood volumes per hectare has been included on a second y-axis.

response, however, this volume was only maintained up until 63% defoliation before a reduction in stand wood volume (slope:  $-6.5$ , y-intercept:  $795 \text{ m}^3/\text{ha}$ ) was recorded (Fig. 4). The average stand wood volume for all trees on-grown under a type 1 growth response was  $358 \text{ m}^3/\text{ha}$  (range: 226–619) with a gross value of AUD\$ 9655 compared with  $331 \text{ m}^3/\text{ha}$  (range: 50–774) with a gross value of AUD\$ 8930 achieved under a type 2 growth response.

#### 4. Discussion

In a review on the effect of insect defoliation on growth and mortality of trees, Kulman (1971) concluded insect tree damage resulted in mortality, growth loss, rotation delays and increased susceptibility to other insect pests and diseases. In the present study *M. privata* defoliation of 2-year-old *E. nitens* resulted in both tree mortality and growth loss. Pinkard et al. (2006b), found that as little as 20% tree defoliation of 3-year-old *E. globulus* by *Gonipterus scutellatus* resulted in significant reductions in stem growth 12 months after defoliation. Growth impacts should also be interpreted not just on level of defoliation but also the location and timing of defoliation. In eucalypts top of crown defoliation has a more severe impact on growth than bottom of crown defoliation (Pinkard, 2002 for *E. nitens*; Pinkard et al., 2006a for *E. globulus*) and early season defoliation has less impact than late season (Cremer, 1966; Candy, 2000 both for *E. regnans*). For *M. privata*, our outbreak was mid-season and where defoliation levels were low they were more bottom of crown. In our study the removal of 28% of foliage significantly reduced stem volume gains for up to 24 months after defoliation; however increased growth recorded at later measurements meant stem volume 75 months after tree damage was not reduced. Indeed, we found that only tree defoliation of somewhere between 50 and 72% resulted in significantly reduced tree volumes 75 months after tree damage.

More shorter-term artificial defoliation studies have also shown a high level of canopy defoliation is required to significantly reduce tree growth, including Carne et al. (65% defoliation of 3-year-old *E. grandis*, 1974), Candy et al. (100% defoliation of 3-year-old *E. regnans*, 1992), Elek (100% defoliation of 3-year-old *E. nitens*, 1997) and Pinkard and Beadle (70% of the lower crown pruning of 3-year-old *E. nitens*, 1998). Pinkard (2002) found only the removal of 80% of leaf area of 2-year-old *E. nitens* changed the growth trajectory such that long-term growth was likely to be reduced and in the present study only trees that were 90% defoliated continued to have divergent growth trajectories compared to trees that were

10% defoliated. The high level of defoliation required to cause significant reductions in stem volume may be due the trees ability to increase photosynthetic capacity of the remaining and regrowth foliage in *E. nitens* (Pinkard et al., 1998). Such tree responses have previously been demonstrated in young poplar hybrids (Bassman and Dickmann, 1982) and while Hoogesteger and Karlsson (1992) found no increased photosynthetic activity in regrowth foliage in mountain birch, they again demonstrated an increased photosynthetic rate in foliage remaining after defoliation.

That defoliation by *M. privata* was higher on the initially taller trees is likely to be due to greater oviposition, a trend opposite to that observed for oviposition by the leaf beetle *Parposisterna* (= *Chrysophtharta*) *agricola* (Chapuis) on *E. globulus* (Rapley et al., 2004). However, there was no significant difference between defoliation classes in initial tree diameter or volume. After a defoliation event tree volume can be affected by either a reduction in diameter growth and/or a reduction in height growth. For all defoliation classes tree diameter growth was proportionally more affected than tree height growth, suggesting the stem of more defoliated trees became narrower in shape. This result was consistent with comparisons between diameter and height growth measurements made following different pruning levels of *E. nitens* (Pinkard and Beadle, 1998; Pinkard, 2002) and *E. grandis* (Lückhoff, 1967), as well as following artificial defoliation of *E. nitens* (Elek, 1997) and the evergreen *Pinus resinosa* (Krause and Raffa, 1996) and beetle defoliation of *E. regnans* (Elliott et al., 1993).

Wood density and growth rate are the most important factors determining the profitability of wood production (Greaves et al., 1997). Therefore, reductions in growth rates can have serious effects on the profitability of a plantation. In the current study the *E. nitens* growth model NITGRO (Candy, 1997) was used to on-grow trees using two growth response scenarios to calculate the upper (type 1 growth response) and lower (type 2 growth response) limits of stand wood volumes at harvest. These predicted stand wood volumes were derived from on-growing individual trees and should be viewed with some caution, as Candy (1997) points out that the scaling-up of individual tree growth impacts to stand-level impacts are subject to large errors. Indeed it is reasonable to expect that stand-level impacts would be less than cumulative individual tree impacts in stands with mixed defoliation because of the accentuating effect of competition.

Some clarification of individual tree growth impacts can be achieved by determining whether tree growth rate after damage was temporarily (type 1 growth response) or indefinitely reduced (type 2 growth response). As realised data was collected for 75 months after tree damage a confident prediction regarding tree growth patterns between the last inventory and harvest can be made. Volume gains for trees 90% defoliated seem to correspond to a type 2 growth response, as they continued to diverge from the 10% defoliation class in all subsequent measurements following the initial 4 month measurements. It is also expected that these trees will become even more suppressed with the onset of canopy closure (Binkley et al., 2002). However, for trees 28 and 50% defoliated, volume gains appear to approximate a type 1 growth response. For these two defoliation classes the initial reduction in their growth rates was not sustained beyond 24 months after tree damage leading to no reduced stem volume, relative to the 10% defoliation class, 75 months after tree damage. The growth response of trees that were 72% defoliated could neither be classified as a type 1 nor 2 response. This is because, their gains in volume, while reduced, were not significantly less compared with the more lightly defoliated trees after 75 months, as expected in a type 1 growth response. Continued growth suppression from the time trees were damaged did, however, result in realised volumes being significantly less compared with more lightly defoliated trees,

reflecting a type 2 growth response. Indeed, trees that were 72% defoliated only had 70% of the wood volume of the 10% defoliated trees. Continued monitoring of tree growth may in time elucidate the type of growth response this level of defoliation causes.

Given the growth responses recorded 75 months after tree damage it appears an economic damage level (Pedigo, 2002) occurs somewhere between 50 and 72% of tree defoliation in the studied plantation. That is if an outbreak of *M. privata* is not going to result in more than 50% tree defoliation it would be uneconomical to control (using an aerial application of insecticide), however if defoliation was predicted to be greater than 50% and further resulted in trees displaying a type 2 defoliation response, aerial spraying would be appropriate. It is however difficult for a plantation manager to predict the level of defoliation that might occur during the initial stages of a pest insect infestation. A threshold for the number of egg batches and larval clutches per shoot that result in potentially damaging populations of the eucalypt defoliating leaf beetle *Paropsisterna* (= *Chrysophtharta*) *bimaculata* (Olivier) has been determined (Elliott et al., 1992). Chrysomelinae beetles are the most frequently observed pest insects in Tasmanian eucalypt plantations (de Little et al., 2008), but similar thresholds for other forest insect pests, including *M. privata*, are still to be calculated. Such thresholds are also complicated by variables such as initial tree/branch egg and larval clutch load, tree vigour, timing of attack, weather conditions and the activity and level of natural enemies. The decision to spray is further complicated by the fact that it will reduce or eliminate natural enemies of the pest (Loch, 2005) and if these beneficial arthropods take longer to recover than that of the pest insect, the plantation manager may be locked in to spraying season after season (Floyd and Farrell, 2007). This is because multiple or chronic defoliation of *E. regnans* (Cremer, 1966; Candy et al., 1992), *E. globulus* (Collett and Neumann, 2002) and *E. marginata* (Wills et al., 2004) have been shown to have a greater deleterious effect on tree growth than occurs with a one-off defoliation event. Despite the difficulties in determining a relationship between the number of *M. privata* egg batches oviposited and the level of tree defoliation caused from the resulting larvae, the determination of such a relationship is seen as important future research. This is because a plantation manager would be able to predict potential tree defoliation by undertaking a survey of egg batches oviposited, thus providing an early indication on whether an outbreak could reach an economic damage level (i.e. 50–72% *E. nitens* defoliation; present study) and hence require chemical control.

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## References

- Abbott, I., 1993. Insect pest problems of eucalypt plantations in Australia. 6: Western Australia. Aust. For. 56, 381–384.
- AFFA, 1997. Plantations for Australia: the 2020 vision. <http://www.affa.gov.au>.
- Bassman, J.H., Dickmann, D.I., 1982. Effects of defoliation in the developing leaf zone on young *Populus × euramericana* plants. I: Photosynthetic physiology, growth, and dry weight partitioning. For. Sci. 28, 599–612.
- Bassman, J.H., Dickmann, D.I., 1985. Effects of defoliation in the developing leaf zone on young *Populus × euramericana* plants. II: Distribution of <sup>14</sup>C-photosynthate after defoliation. For. Sci. 31, 358–366.
- Binkley, D., Stape, J.L., Ryan, M.G., Barnard, H.R., Fownes, J., 2002. Age-related decline in forest ecosystem growth: an individual tree, stand structure hypothesis. Ecosystems 5, 58–67.
- BRS, 2009. Australia's Forests at a Glance 2009. Bureau of Rural Sciences, Canberra.
- Candy, S.G., 1997. Growth and yield models for *Eucalyptus nitens* in Tasmania and New Zealand. Tasforests 9, 167–198.
- Candy, S.G., 2000. Predictive models for integrated pest management of the leaf beetle *Chrysophtharta bimaculata* in *Eucalyptus nitens* plantations in Tasmania. Ph.D. thesis. School of Agricultural Science, University of Tasmania, 472 pp.
- Candy, S.G., Elliott, H.J., Bashford, R., Greener, A., 1992. Modelling the impact of defoliation by the leaf beetle, *Chrysophtharta bimaculata* (Coleoptera: Chrysomelidae), on height growth of *Eucalyptus regnans*. For. Ecol. Manage. 54, 69–87.
- Carne, P.B., Greaves, R.T.G., McInnes, R.S., 1974. Insect damage to plantation grown eucalypts in north coastal New South Wales, with particular reference to Christmas beetles (Coleoptera: Scarabaeidae). J. Aust. Entomol. Soc. 13, 189–206.
- Collett, N.G., Neumann, F.G., 2002. Effects of simulated chronic defoliation in summer on growth and survival of blue gum (*Eucalyptus globulus* Labill.) within young plantations of northern Victoria. Aust. For. 65, 99–106.
- Cremer, K.W., 1966. Effects of partial defoliation and disbudding on height growth of *Eucalyptus regnans* saplings. Aust. Forest Res. 6, 41–42.
- de Little, D., Foster, S., Hingston, T.L., 2008. Temporal occurrence pattern of insect pests and fungal pathogens in young Tasmanian plantations of *Eucalyptus globulus* Labill. and *E. nitens* Maiden. Pap. Proc. R. Soc. Tasman. 142, 61–69.
- Elek, J.A., 1997. Assessing the impact of leaf beetles in eucalypt plantations and exploring options for their management. Tasforests 9, 139–154.
- Elliott, H.J., Bashford, R., 1978. The life history of *Mnesampela privata* (Guen.) (Lepidoptera: Geometridae) a defoliator of young eucalypts. J. Aust. Entomol. Soc. 17, 201–204.
- Elliott, H.J., Bashford, R., Greener, A., 1993. Effects of defoliation by the leaf beetle, *Chrysophtharta bimaculata*, on growth of *Eucalyptus regnans* plantations in Tasmania. Aust. For. 56, 22–26.
- Elliott, H.J., Bashford, R., Greener, A., Candy, S.G., 1992. Integrated pest management of the Tasmanian *Eucalyptus* beetle, *Chrysophtharta bimaculata* (Olivier) (Coleoptera: Chrysomelidae). For. Ecol. Manage. 53, 29–38.
- Farrow, R.A., Floyd, R.B., Neumann, F.G., 1994. Inter-provenance variation in resistance of *Eucalyptus globulus* juvenile foliage to insect feeding. Aust. For. 57, 65–68.
- Floyd, R.B., 1997. Breeding resistance in eucalypts to insect attack. Trees Nat. Resour. 16–19.
- Floyd, R., Farrell, G., 2007. General discussion and summary. In: Floyd, R., Farrell, G. (Eds.), Impact of Insects on Eucalypt Plantations in the Murray Valley. Rural Industries Research and Development Corporation, Barton, pp. 127–147.
- Forestry Tasmania, 2007. Long term pulpwood supply agreement between Forestry Tasmania and Gunns Limited. <http://www.forestrytas.com.au/forest-management/wood-supply-agreements>.
- Greaves, R., 1966. Insect defoliation of eucalypt regrowth in the Florentine Valley, Tasmania. Appita 19, 119–126.
- Greaves, B.L., Borralho, N.M.G., Raymond, C.A., 1997. Breeding objective for plantation eucalypts grown for production of kraft pulp. For. Sci. 43, 465–472.
- Hodge, G.R., Volker, P.W., Potts, B.M., Owen, J.V., 1996. A comparison of genetic information from open-pollinated and control-pollinated progeny tests in two eucalypts species. Theor. Appl. Genet. 92, 53–63.
- Hoogesteger, J., Karlsson, P.S., 1992. Effects of defoliation on radial stem growth and photosynthesis in the mountain birch (*Betula pubescens* ssp. *tortuosa*). Funct. Ecol. 6, 317–323.
- Jenkin, B., 1990. Eucalypt plantation silvicultural regimes. 1990 Gottstein Fellowship Report. J.W. Gottstein Memorial Trust Fund, Clayton, Vic., Australia, 137 pp.
- Jordan, G.J., Potts, B.M., Chalmers, P., Wiltshire, R.J.E., 2000. Quantitative genetic evidence that the timing of vegetative phase change in *Eucalyptus globulus* ssp. *globulus* is an adaptive trait. Aust. J. Bot. 48, 561–567.
- Jordan, G.J., Potts, B.M., Clarke, A.R., 2002. Susceptibility of *Eucalyptus globulus* ssp. *globulus* to sawfly (*Perga affinis* ssp. *insularis*) attack and its potential impact on plantation productivity. For. Ecol. Manage. 160, 189–199.
- Krause, S.C., Raffa, K.F., 1996. Differential growth and recovery rates following defoliation in related deciduous and evergreen trees. Trees 10, 308–316.
- Kulman, H.M., 1971. Effects of insect defoliation on growth and mortality of trees. Annu. Rev. Entomol. 16, 289–324.
- Landsberg, J., Ohmart, C., 1989. Levels of insect defoliation in forests: patterns and concepts. Trends Ecol. Evol. 4, 96–100.
- Loch, A.D., 2005. Mortality and recovery of eucalypt beetle pest and beneficial arthropod populations after commercial application of the insecticide alpha-cypermethrin. For. Ecol. Manage. 217, 255–265.
- Lückhoff, H.A., 1967. Pruning of *Eucalyptus grandis*. For. South Africa 8, 75–85.
- Lukacs, Z., 1999. Phenology of autumn gum moth *Mnesampela privata* (Guenée) (Lepidoptera: Geometridae). Ph.D. thesis. School of Agricultural Science, University of Tasmania, 252 pp.
- MacArthur, R.H., 1957. On the relative abundance of bird species. Proc. Natl. Acad. Sci. U. S. A. 43, 293–295.
- Matsuki, M., Farrow, R.A., Floyd, R.B., 2007. Effects of acute damage and chronic damage by insects on growth in *Eucalyptus globulus*. In: Floyd, R., Farrell, G. (Eds.), Impact of Insects on Eucalypt Plantations in the Murray Valley. Rural Industries Research and Development Corporation, Barton, pp. 56–69.
- Mercer, D., Underwood, A., 2002. Australian timber plantations: national vision, local response. Land Use Policy 19, 107–122.

- McQuillan, P.B., 1985. A taxonomic revision of the Australian autumn gum moth genus *Mnesampela* Guest (Lepidoptera: Geometridae, Ennominae). *Entomol. Scand.* 16, 175–202.
- Neumann, F.G., Collett, N.G., 1997. Insecticide trials for control of the autumn gum moth (*Mnesampela privata*), a primary defoliator in commercial eucalypt plantations prior to canopy closure. *Aust. For.* 60, 130–137.
- Pedigo, L.P., 2002. *Entomology and Pest Management*. Prentice Hall, New Jersey.
- Pinkard, E.A., 2002. Effects of pattern and severity of pruning on growth and branch development of pre-canopy closure *Eucalyptus nitens*. *For. Ecol. Manage.* 157, 217–230.
- Pinkard, E.A., Battaglia, M., 2001. Using hybrid models to develop silvicultural prescriptions for *Eucalyptus nitens*. *For. Ecol. Manage.* 154, 337–345.
- Pinkard, E.A., Beadle, C.L., 1998. Effects of green pruning on growth and stem shape of *Eucalyptus nitens* (Deane and Maiden) Maiden. *New Forest* 15, 107–126.
- Pinkard, E.A., Beadle, C.L., Davidson, N.J., Battaglia, M., 1998. Photosynthetic responses of *Eucalyptus nitens* (Deane and Maiden) Maiden to green pruning. *Trees* 12, 119–129.
- Pinkard, E.A., Baillie, C.C., Patel, V., Paterson, S., Battaglia, M., Smethurst, P.J., Mohammed, C.L., Wardlaw, T., Stone, C., 2006a. Growth responses of *Eucalyptus globulus* Labill. to nitrogen application and severity, pattern and frequency of artificial defoliation. *For. Ecol. Manage.* 229, 378–387.
- Pinkard, E.A., Baillie, C., Patel, V., Mohammed, C.L., 2006b. Effects of fertilising with nitrogen and phosphorus on growth and crown condition of *Eucalyptus globulus* Labill. experiencing insect defoliation. *For. Ecol. Manage.* 231, 131–137.
- Rapley, L.P., Allen, G.R., Potts, B.M., 2004. Genetic variation in *Eucalyptus globulus* in relation to susceptibility from attack by the southern eucalypt leaf beetle, *Chrysophtharta agricola*. *Aust. J. Bot.* 52, 747–756.
- Snowdon, P., 2002. Modeling type 1 and type 2 growth responses in plantations after application of fertilizer or other silvicultural treatments. *For. Ecol. Manage.* 163, 229–244.
- Steinbauer, M.J., 2002. Oviposition preference and neonate performance of *Mnesampela privata* in relation to heterophylly in *Eucalyptus dunnii* and *E. globulus*. *Agric. For. Entomol.* 4, 245–253.
- Stone, C., 2001. Reducing the impact of insect herbivory in eucalypt plantations through management of extrinsic influences on tree vigour. *Austral Ecol.* 26, 482–488.
- Wills, J.A., Burbidge, T.E., Abbott, I., 2004. Impact of repeated defoliation on jarrah (*Eucalyptus marginata*) saplings. *Aust. For.* 67, 194–198.